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DARWIN'S WORK ON MOVEMENT IN PLANTS

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It is remarkable, when one considers the central interest of Darwin's life, that he should have found time and strength to devote so considerable a portion of his energy to purely botanical work. It is natural and fitting at this time that the major interest of the world should be directed to his larger achievements, but it should not be lost sight of that his botanical work alone represents no small labor accomplished. We may indeed not always agree at present with his conclusions and may differ even as to actual observations, but the fact remains that he developed a number of highly important topics relating to plant behavior.

His lines of investigation among plants were indeed somewhat special, for he made no pretence of covering completely the field of even that side of botany which interested him, but simply investigated certain more or less important phases of plant life that came under his notice. It may be expressed, perhaps, by saying that his botanical studies were his avocation, and were employed by him in a measure as a recreation from the exactions exercised by his larger tasks. That does not mean, however, that there was anything dilettantish in the spirit of his attack on botanical problems or that his work along these lines was not as thorough as his circumstances permitted. Thoroughness indeed was an important element in all that Darwin undertook and the patient application to even small details is the secret of much of the value of these botanical studies.

From his published letters it would seem that his work with plants was to him of the nature of a pastime, serious indeed but none the less a pastime, in which he often found himself so interested that all other lines of intellectual activity were for the time forgotten. Possibly what first inclined him to study plants was the delight of observation and experiment to which he so keenly reacted, for, placed as he was in the country and in none too good health, these faculties found their easiest and most natural outlet in his garden. Even when he was least well, so long as he was able to exert any effort at all, his plants claimed his interest and one of his friends speaks of how in the daily walk about the garden path there was always some experiment or some particular plant which was to be watched and noted.

He did not himself make any claim to being a trained botanist and, without in any way reflecting upon the value of the work which he did, it must be admitted that he was not. He freely asked help of his botanical friends and freely it was given.

Most of his botanical contributions were published in book form and it is to be noted that they had a relatively wide circulation for books of a special character, a fact which speaks well for the manner of treatment and general interest of the subjects about which he wrote. Of these works there are three which especially concern the subject of this address and these are as follows: ''Insectivorous Plants'' published in 1875, ''The Movements and Habits of Climbing Plants'' which appeared first in 1865 in the *Journal of the Linnean Society* and was afterwards printed in book form, and ''The Power of Movements in Plants'' which bears the date of 1880. It is not the intention to take these up seriatim or discuss each detail, but rather to point out what seem some of the more important and crucial aspects of the various subjects treated therein.

Perhaps the most important single fact that Darwin elucidated was that of the universality of the oscillations of the growing points of plant members. This he termed circumnutation, a word now generally adopted; and by it he meant the swinging motion of plant extremities as they progress through space, due to inequalities of growth. He was not indeed the first to observe individual instances of either periodic or ephemeral movements of a more or less pronounced degree, but to him belongs the credit of first insisting upon the fact that all growing organs describe a more or less spiral orbit. He developed this idea with such enthusiasm that he carried his line of thought to extremes and concluded that all plant movements were but modifications and adaptations of circumnutatory motions. Only in the cases of the motions of Mimosa leaves and Drosera tentacles did he express his doubt as to the applicability of the principle of circumnutation to all plant movements. He included all forms of tropisms, contact responses, other than those named, under this one head. In the final chapter of "The Power of Movement in Plants" he says:

> It has been shown that the following classes of movement all arise from modified circumnutation, which is omnipresent whilst growth lasts, and after growth has ceased, whenever pulvini are present. These classes of movement consist of those due to epinasty and hyponasty,—those proper to climbing plants, commonly called revolving nutation, the nyctitropic or sleep movements of leaves and cotyledons, and the two immense classes of movement excited by light and gravitation.

In the next paragraph he excepts the contact movements of Mimosa and Drosera, already referred to, saying:

> Although so many movements have arisen through modified circumnutation, there are others which appear to have a quite independent origin; but they do not form large or important classes.

When we consider the nature of the man and reflect that the whole trend of his mind was towards the concept of unity in the organic world it does not seem extraordinary that he should have taken such an attitude; an attitude too that was helped on by the extreme simplicity of his methods of experimentation. The very fact that he approached the question with a mind entirely free from bias had its advantages, but it also brought a greater chance of being too easily swayed by his own point of view. It must be remembered also that the distinction between autonomous and induced or paratonic movements was not so sharply drawn then as it is now. At present we place the tropistic movements due to whatsoever external cause, under the general class of aitonomic movements, in contradistinction to circumnutation, epinasty, hyponasty and so forth, which we are pleased to term autonomic or due to internal causes. In the latter class, it must be confessed, the relegation of movements to autonomous causes is often a mere confession of ignorance, as is well instanced by the older opinion first advanced by Darwin that the twining of stem climbers is wholly autonomic. It is only in the sense that the movements of fixed plant organs are in the vast majority of cases ultimately due to unequal growth changes that we can say that circumnutation is the fundamental process concerned. In other words, it is only if we were to define circumnutation as the power of plant parts to show either unequal turgescence or unequal growth that we could accept the universality of Darwin's statement.

As far as his observations on circumnutation proper are concerned, or, as he would have termed it, unmodified circumnutation, his conclusions are of the highest value, and form even to the present day really a large part of our literature on the subject. By the simplest means he plotted the orbits, so to say, of a very considerable number of growing tips. Entirely aside from any especial interpretation to be placed upon them, his descriptions of the behavior of seeds during germination and of the growth of seedlings, give a clear and accurate account of the general organography of the adolescent plant.

In another very important direction were the researches of Darwin rewarded by far-reaching results; namely, in the matter of the transmission of stimulus in plants. Until the publication of his experiments it had been largely overlooked that there might be a separation in space between the percipient and motor zone in tropic responses. It is true, no doubt, that some of his methods and even some of his conclusions were faulty, but nevertheless the credit belongs to him for establishing a point of departure from which further developments of first importance have come. The demonstration of so fundamental a fact has had no inconsiderable influence in the understanding and interpretation of sense perception among plants.

Although many observers at first contended against the possibility of such a propagation of stimulus and denied the accuracy of Darwin's results, yet the general correctness of his statements has been established even though differences in interpretation may have crept in. One reason, no doubt, why it was difficult to admit and support Darwin's conception and to corroborate his results, is that the region capable of perceiving a stimulus is so localized and the conduction to the responsive area is over so short a distance. One may gather from his writings that he did not regard the response to stimuli in the nature of a release of a regulatory mechanism, as it is now so commonly understood: his point of view indeed as to the nature of such tropic responses as being merely a modified form of circumnutation was against such an interpretation. His attitude was of course that of the teleologist, for he was ever keen to uncover purpose in the reaction of organisms. In his concluding remarks and summaries, while he suggested the interpretation of such responses along the line of consciousness he exhibited a considerable reserve and went no farther than indicating the appropriateness of a comparison of the similarity to the responses in lower animals. He did not enter largely into the somewhat fruitless field of the philosophical discussion of the question. His reserve possibly but reflects the greater caution of a past generation in interpreting protoplasmic response universally in terms of what we know about the problem in higher animal forms, but be that as it may, one is inclined to the opinion that it was Darwin's own reluctance to commit himself too unreservedly which restrained him, for in other matters he has amply shown that he was not afraid to combat what to him were mere conventionalities.

A large portion of his book on climbing plants is devoted to a consideration of the tendril bearers and takes up a wide range of forms. The exceeding sensitiveness of these organs to contact Darwin was one of the first to appreciate, but he went somewhat astray in supposing that mere pressure was enough to induce the characteristic coiling response. It was not thoroughly understood until later that weight alone is not sufficient, but that the stimulus must involve some more intricate contact shock. He did not understand that the exciting body must have a certain degree of what one may call roughness and consequently he did not understand the inaction of tendrils to raindrops.

His conclusions did not wholly agree with the now accepted explanations of the nature of the response of tendrils but it inclined to the view that the rapid reply of incurving tendrils was primarily caused by turgor changes ultimately rendered permanent by growth. More recently it has again been claimed that the curvature is wholly a growth phenomenon, but in so much as turgor changes are often apparently so greatly concerned with the first stages of cell enlargement incident upon growth, may not the initial curvature be after all a matter of unequal turgor pressure on the two sides of the tendril? Here as in other places Darwin considered the response of contact stimulus a form of modified nutation.

Although Drosera and similar plants were not considered by Darwin in this connection, in so much as some phases of his study had to do with their response to contact irritation, it is suitable to introduce the matter now. His investigation of the behavior of Drosera was especially detailed and represented at the time a great advance in the knowledge of the habits of this insectivorous form. There is not, as a matter of fact, any more elaborate or complete study at present, although his results were published some thirty years ago. Many important observations were made by him, especially that the gland at the tip of a tentacle is exclusively the sensitive region and that a stimulus can be propagated down the central tentacles and along to and up the adjacent ones. Although he made most careful and repeated examination of the protoplasmic behavior as the stimulus progressed, and noted some curious changes which take place in the protoplasm of the responding tentacles, yet he was unable to advance any explanation of the physics of the process. Indeed, none has been offered since and much that Darwin said is still the last word on the subject.

Extending his work from the effect of mechanical stimuli to chemical ones, Darwin showed that many substances of very various kinds could effect a very vigorous response. He was, indeed, the first to make an endeavor at a close study of the insectivorous or rather carnivorous plants. Not only were his observations on the inflection of the tentacles of Drosera and the trapping of insects by this and other forms largely new; but also, and what was more important, perhaps, his investigations into the digestive action of their secretions were really the first in the field. His experiments along this line were especially exhaustive; and, with the exception of some details later writers have done little by way of correction or amendment. He did not it is true, isolate any specific enzymes but nevertheless we came to the conclusion that a pepsin-like enzyme was excreted by these plants, which enables them to digest external proteid material. He also noted the rennet-like action of the excretion in Drosera and arrived at the just conclusion that the curdling of milk due to the latter could not come from the acidity of the excretion alone, though at that time little or nothing was known concerning vegetable rennets. It is not to be wondered, when one considers the lesser acquaintance which was then possessed of ferments in general and plant enzymes in particular, that Darwin did not further discuss or attempt to investigate the enzymes which he had discovered and to determine whether they were peptic or tryptic or whether the curdling power was due to a specific enzyme, apart from the others.

The complexity of ferment action and the possible coexistence of several distinct enzymes in one secretion was not fully appreciated at that time, and working as Darwin of necessity did, he was not in close enough touch with these matters as they then stood to branch out on his own account into very new fields. What he did do was to make a careful and pretty exhaustive empirical study of the action of the excretion of the glands on a great range of substances. If his list of the latter included a number which were immaterial by way of affording new light on the question and a few which, owing to their mode of preparation, gave inconclusive or erroneous results, it matters very little. He proved successfully the main thesis which he maintained, namely, the ability of these insectivorous plants to avail themselves of proteids as food. When one considers how much even to-day in the study of enzymes depends on almost pure empiricism and what valuable results have in the past been obtained by such methods, one does not cavil at Darwin's mode of attack, although at times it may impress one as a bit happy-go-lucky.

As a detailed study of the habits of an organism his extended observations on Drosera stand out as a masterpiece of this kind of work and the collective result of this work may justly be regarded as one of his best pieces of botanical investigation. It is evident from his letters that he took the keenest interest in this plant, which apparently stimulated his imagination and his desire towards investigation as much as any one thing which came under his notice. It was a subject peculiarly well fitted for his type of investigation, for in it he did not require elaborate mechanical aid to arrive at important results and the previous literature on the subject was scanty and for the most part of minor importance. He had an almost clear field and made the most of his opportunity by producing a work which must for all time remain the basis of our knowledge of these interesting forms. He pushed it as far as his means at hand permitted, and while in many points he could not arrive at definite conclusions, it is a fact that most of his unanswered questions are unanswered still. While his knowledge of plant physiology may not have been broad enough for him to correlate this special form of nutrition, with the general problems of plant metabolism it is to be remembered that after all it was not from such a standpoint that he took up the problem.

There is one characteristic which is particularly admirable in all of Darwin's botanical work and that was his endeavor in so far as he could to examine an abundance of different forms which would illustrate any topic under investigation. This is the more to be remarked since he was not really very fortunately placed in the matter of obtaining material. For keeping his plants after he had obtained them he had to depend entirely upon such facilities as his own garden and greenhouse afforded. Being unable himself to collect material to any extent, he had to depend upon the generosity of his friends and correspondents, who, it may be said, responded with alacrity. None but one of very active mind and great perseverance would have accomplished what he did in an experimental way under the difficulties which beset him, and his work affords a good example of how a relatively large amount can be accomplished by even a little time given continuously. Entirely aside from any absolute value which these books may have, they were an important contribution at that stage in the development of plant physiology, to the literature on the subjects on which they touched. No man with a less well developed faculty for detail and continued effort could have kept the thread of the work so well, despite the many interruptions to which it was subjected. Their value, it may be said, is more to botanical science than a merely sentimental one—it is rather in many respects one of real achievement.

It has been stated that one of the greatest services rendered by Darwin to the study of natural history was the revival of teleology. The presence of this mode of thought in his work shows no better anywhere than in his work on the movements of plants, where it apparently afforded to him one of his liveliest interests. In the light of the present disfavor into which teleological interpretations have fallen these statements, which are indeed in accord with the mental attitude of Darwin, require some comment. It is not that one need raise one's voice in favor of teleology as such, to apologize for his purposeful explanations of the form and function of organs; but it should in justice be said that it is where teleological evidence and teleological reasoning are accepted as a finality or where they lead to prejudgment that the most mischief is done. Darwin's whole make-up and trend of thought was such as to make him turn to immediate causal explanations for natural phenomena and he unquestionably was a teleologist, but in the main his interpretations were tempered by common sense, intellectual reserve and balanced judgment. It has been rightly said, too, that his teleology had a far wider and more coherent plan than that of his predecessors and it may be added it was less positive than that of some of his contemporaries and some of those that followed him.

It is wholly natural that with a mind like his, which ranks him with the greatest correlaters and unifiers of loose facts that the world has known he should also have attempted to unify the explanations of the phenomena examined in his botanical researches and his position as to the fundamental nature of circumnutation was no doubt a result of his temperamental attitude towards large questions. But while we need not necessarily follow him in all of his generalizations the fact remains that he did no inconsiderable service to botanical science if in no other way than, at least, in showing what may be learned from the close and careful examination of the plant as a living organism.

In a final summing up of Darwin's studies that have come under discussion here, perhaps a fair statement may be made by saying that he investigated, as accurately as both his knowledge and his facilities for experimentation allowed, a large range of plant forms which illustrated the especial subjects in which he was interested; that he discovered or drew attention to many important facts, either previously unknown or neglected regarding the habits of the plant forms which he had under observation; that if his interpretations were at times faulty, his observations were in the main accurate; and that he revivified subjects which had often times become only of more or less academic interest. Darwin himself—none better—recognized that many of his experiments must be unsatisfactory and his explanations merely tentative; and he was ready enough to accept correction which appeared to him justified. The very fact that he brought to his botanical researches a mind fresh and unprejudiced lends a peculiar value to his work. Unhampered by tradition and with an open mind, he interpreted the facts as he saw them, and we must remember that some of our criticisms may be in part due merely to the greater complexity of our own interpretations, than to any absolute superiority of them. Despite the advances which have been made, it should not be forgotten that Darwin's influence was in the direction of sound investigation; and we should not pass over ungratefully this phase of plant physiology from which has come much that is of the first importance to-day. As a stimulus to later investigators Darwin's work, whether in botany alone or in other fields, has had a profound influence on the plant physiologist though he may not always recognize it. It would be our shame if we could not have improved over the concepts of the science as current in Darwin's time, and our misfortune if we think that these betterments are not capable of as relatively great advance in the future.